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TERTIARY NYMPHALID BUTTERFLIES
AND SOME PHYLOGENETIC ASPECTS OF SYSTEMATIC LEPIDOPTEROLOGY

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MOST ZOOLOGISTS AND GEOLOGISTS agree that the phylogeny should represent evolutionary relationships between various organic groups, and that the genuine test of validity for any phylogenetic construction must be based on evolutionary data from different time periods. With a few exceptions, all neozoological constructions poorly express the real phylogeny in the considered groups. Rather, they show primarily immediate inheritance — successive transitions between forms that live at the same time, the recent epoch. What is detected stage by stage is the provisory origin of the groups of various taxonomic rank. And however rich may be the material, however deeply it may be studied, one of the fundamental phylogenetic and evolutionary problems must always be left unsolved by the *neo*zoologist — that of the direction of evolution.

Recent Rhopalocera are one of the most studied insect groups. Only the most remote areas of Asia and South America are able to supply the Lepidopterists of today with any important new finds. The great amount of material, accumulated by numbers of student generations, has been subjected to phylogenetic interpretation by numerous authors. In the course of study, various characters and groups of characters were considered. But in spite of good, and sometimes excellent, knowledge of these insects in almost every aspect, the problem of their basic phylogeny still remains open.

The key to this problem must be sought in fossil remains. Yet among the fossil Lepidoptera, imprints of Rhopalocera are exceptionally rare even though their body seems to be strong enough for good preservation in deposits of various types. One possible explanation for the rarity of butterfly finds is that the smaller quantity of Rhopalocera, compared to all the various groups of Heterocera, decreases the probability of finding their remnants.

Taking into account the described difficulties of lepidopterological phylogenetics that arise from the lack of fossil material, it is easy to imagine the value of each paleontological find in this group. The study of such rarities, perhaps not of particular interest for a geologist, is extremely important for a student of Lepidoptera. That is why I undertook with great joy the study of materials (imprints) that were kindly forwarded to me from the Paleontological Institute, Academy of Sciences, U.S.S.R. (Moscow).

Described material has been found in Karagan (Miocene) continental deposits near Stavropol (North Caucasus), in a locality Vishnevaya Balka (Cherry Ravine) which is abundant with insect imprints. Insect-containing layers from this area have been discovered in 1938 by B. F. Kaspiev (1939), and faunistically characterized in 1939 by B. B. Rohdendorf.

Kozhanchikov described *Xyleutites miocenicus* in 1957 from these deposits. Insect-containing layers, as determined by B. F. Kaspiev, are connected with upper horizons of the Karagan stage where fragile rocks alternate with gray sandy clays. Taphonomically* studied pieces are characterized by very high exactness that is the result of the fine grain structure of the containing rock. On the other hand, the high fragility of the rock caused the fragmentation of all pieces, and in the material studied no complete wings were found. Yet the venation pattern was sufficiently complete in one of the imprints to give it great diagnostic value.

Method of Treatment and Comparison of the Material

The mentioned lack of fossil Rhopalocera excluded any possibility of comparison of the considered specimens with corresponding specimens from other deposits and different ages. The only material which served for comparative purposes were specimens of recent species. In order to increase the objectivity, comparisons have been made not with the wings of recent butterflies, but rather their impressions on plasticine. The method involves the pressing of separated wings into a plasticine block. It may be done by a press shown in Figure 1, or by metal or glass plates. In order to prevent the plasticine block from sticking to the plate or press, sheets of glassine paper are placed between the block and other parts of this system. These sheets are re-

*For definition of "taphonomy" see I. A. Efremov (1950).

moved after use. After taking out the impressed wing, a very exact impression of the veins remains inscribed in contour on

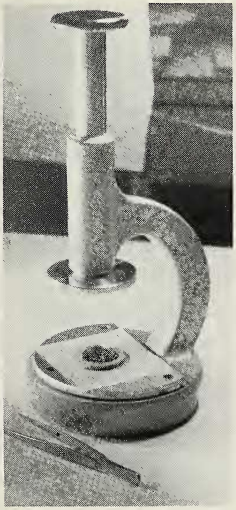

Fig. 1. Press used to obtain plasticine block impressions.

the plasticine block. On these impressions, however, the veins turned out somewhat thicker than in either the wing that was pressed, or the geological imprint. It may be that as a result of pressure, the veins are somewhat deformed and increase their surface area of contact with the plasticine block. Under the action of pressure, some wing scales are impregnated into the block surface; this, to a certain degree, also preserves the color and wing-pattern on the imprint. Though this method has as its main deficiency the loss of the treated wing, it allows a proper comparison: geological and artificial imprints, rather than imprints and actual wings. The described method seems to be more objective as the venation looks quite exact on the imprints; it is not covered with scales of tousled hairs. As to the loss of materal, here two points must be taken into account. First, collecting in the field, the Lepidopterist often collects specimens whose condition is too poor for the collection, but which are suitable to produce imprints. Second, usage of even material from the museum collection for this purpose is, I strongly believe, completely justified by the importance of the task.

It is interesting to begin the comparison with a biometric study. But in all specimens the distal part of the wing is absent, so until additional data is available, the absolute size of these fossil wings must be measured using an approximation. For good accuracy, statistically, a series of material would have been needed. However, is is possible to state now that their size is comparable with recent representatives of Vanessa. In both specimens the proximal part of three vein systems is well preserved, which makes it possible to obtain the following measurements: (Figure 2)

1. D_1 — distance between base of M_2 and anostomosis of M_1 and R
2. b – distance between bases of C_1 and C_2
3. c — distance across the central cell between the bases of $M_3 + C_1$ and $\frac{M}{M_1}$
4. c_1 — Same as c except measured between R and C_2
5. d — distance between bases of S and R

A review of lengthy series of recent material in this group gave hope of obtaining reliable data for these measurements,

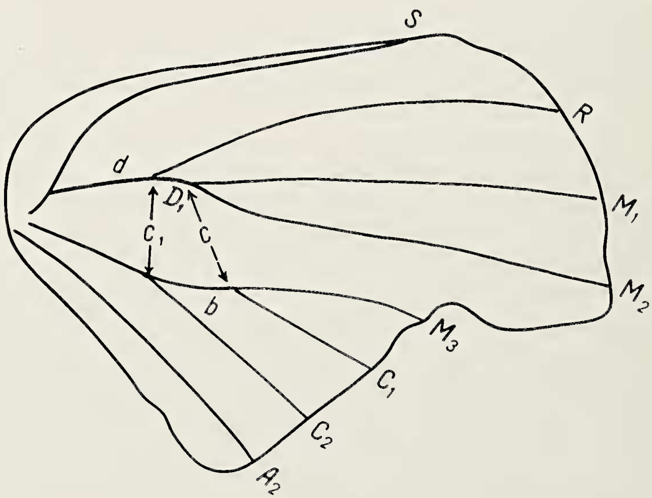

Fig. 2. Venation of *Vanessa karaganica,* n. sp.; definition of measurements used in comparisons.

though it must be noted that venation knowledge of recent Rhopalocera is still at a very low level in both the resultative and methodical senses. Due to the lack of detailed knowledge of the wing venation of recent butterflies, it is difficult to choose reliable characters in the venation for the purpose of paleontological and comparative-morphological survey.

DESCRIPTION OF A NEW FOSSIL SPECIES:

Family: *NYMPHALIDAE*

Swains. Phil. Mag., Ser. II, Vol. I: 187 (1827);
Westw. Genera Diurn. Lep.: 143 (1852)

Genus: *VANESSA Fabricius*

Illiger Mag. f. Insektenkunde, VI: 281 (1807)

Vanessa karaganica, Paleontologicheski Journal (Moscow), 1965, 4:97-99 (In Russian). Nekratenko

Holotype: Paleontological Institute, Academy of Sciences of U.S.S.R., No. 254/2936a; Stavropol, North Caucausus, Vishnevaya Balka, Karagan horizon of Miocene. (Figure 3)

Fig. 3. Holotype of *Vanessa karaganica,* n. sp.

Diagnosis: By venation, type of wing-pattern and habitus, it is closely related to the recent *Vanessa urticae L.*, and differs from the latter by the smooth shape of the termen, without sharp projections or teeth; the most distal point of the dark basal area lies in the cell between M2 and M3 (fig. 3a).

Fig. 3a. Artificial imprint of *Vanessa urticae* L. on plasticine.

Description and Comparative Notes: The central cell is not closed. Venation is typical for the genus *Vanessa*. In comparison with *Vanessa urticae* it is easy to determine that the considered imprint has been made by the left wing with the underside facing the observer. In *Vanessa urticae*, on the upper side, the dark basal spot is limited by the vein M_2; on the underside it occupies the entire basal part of the wing. On the described specimen, several dark spots are found between the basal spot and the marginal elements of the pattern. These spots, mostly between S and R, but also between M_1 and M_2, have not been observed in any artificial or natural variation of *Vanessa urticae*. Comparison of this pattern with the pattern of *Standfuss aberatios* makes it likely that we are dealing with a "hot" form, close to ab. *ichnusa* or *ichnusoides*. Perhaps this last is of paleogeographical importance. These "hot" forms, by the way, are characterized by a more smoothly shaped termen than in the formal forms.

If additional material of fossil *Vanessa* becomes available, there will be chance to carry out a comparative survey of the pattern, which is most interesting in connection with the prototype concept of B. N. Schwanitsch (1949—see references). In the present case it is possible to state that the strial system of the forewing is continued in the hindwing in ancestral forms like *Vanessa karaganica.* The movement of this strial system in the proximal direction is culminated by its full junction with the basal system, giving rise to the dark basal field.

Morphometric data: D_1=1.5 mm, b=2.5 mm, c=4.0 mm, c=4.0 mm,
c_1=3.5 mm, d=4.0 mm.

Remarks: An impression of the incomplete hindwing, oriented to the right hand, on fine grain light shale. On the impression the following veins are clearly visible: P, S, R, M_1, M_2, in their entire length; M_3, C_1, C_2 and A_2 are missing the outer one-fourth of their length.

Occurrence: Upper Miocene, Karagan; North Caucausus, Stavropol Elevation.

Material: Holotype only.

NOTES ON A SECOND FOSSIL SPECIES
Genus *PYRAMEIS* Huebner (?)

Material: Paleontological Institute, Academy of Sciences, U.S.S.R. (Moscow), No. 254/2753, Stavropol, North Caucasus, Vishnevaya Balka. Negative imprint and fragments of positive imprints of hindwing. Impressions on fine grain flinty slate. Distal part of the venation was not preserved. On the imprints traces of single scales are clearly visible. The color of the piece is dark brown. See Figure 4.

Similar venation is found in all large representatives of the group *Vanessidi.* The comparison of this imprint with artificial plasticine imprints of major recent species shows its close relation to the genus *Pyrameis* Hbn., and in the range of this genus to P. *cardui* L.

Measurements have been made by the method shown in Figure 2 and the obtained data compared in the following table. For all recent species the mean sizes of ten specimens are given, except for *P. virginiensis,* of which only one example was available.

The study of the venation of a single specimen will not give a reliable indication of the species to which this specimen belongs. This is due to the incomplete knowledge of venation as a

TABLE 1.

	D_1	b	c	c_1	d
P. fossilis (nomen conditionalis)	1.5	3.5	4.5	4.5	4.0 mm.
P. cardui L.	1.0	3.0	4.5	6.0	4.5 mm.
P. atalanta L.	3.0	4.0	4.0	5.0	4.0 mm.
P. indica Hrb.	5.0	3.5	5.0	5.5	5.0 mm.
P. virginiensis Dru.	0.0	3.0	5.1*	4.0*	4.0 mm.

*Distance across the central cell between anostomoses of R, M_1 $_2$ and the base of C_1 and C_2.

taxonomic character in recent species. Nevertheless, on the basis of a morphometric investigation I believe that the considered specimen is closer to *Pyrameis* than to *Vanessa*. Among all *Pyrameis* considered, this species is the closest to *P. cardui* L. In my opinion, the material here is not complete enough for a new species description, but some preliminary theories will be presented.

The genus *Pyrameis* contains a group of very "eurybiont" species, among which *P. cardui* is noted as the most widely distributed. Because of its great adaptive range, this butterfly is

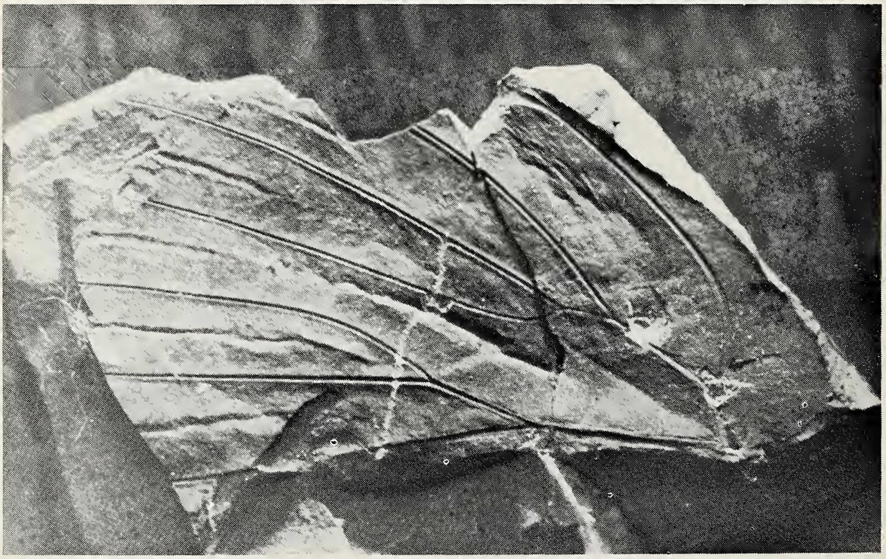

Fig. 4. Fragment of hindwing, *Pyrameis fossilis* (nomen conditionalis).

found nearly throughout the whole globe. It is absent just in the polar areas and, it seems to me, in South America. A. A. Jachontov (1935) noted that there are no differences between specimens from cold and warm areas, with the exception of slight variation in color: "climate to a certain extent affected the wing coloration of them." If a series of *P. cardui* from different countries are placed in the same collection box, then even trained eyes will not recognize their geographic origin. The nine forms of *P. cardui* given by Stichel (1909) does not have any geographical basis and is probably due to the occurrences of butterflies developed in years of great climactic oscillations. As far as I know, they do not differ from each other in any way in venation. As for other species of this genus, they do not manifest so great a tendency to variation as we see in *Satyrus, Parnassius,* etc., though they are more local.

One of the causes of speciation is environment. Interacting with an organism in various ways, it gives rise to development of new forms, and to the decline of old ones, if they are eliminated by their narrow adaptive range. It is also known that geographical variation is the result of heterogeniety of environment over the species' range. In this way, temporal variability must be connected with environmental heterogeniety in time. It is natural to presume that a definite dependence exists between spacial and temporal variability. The most important point here is that an organism's variability is a function of its adaptive range, which evolves together with all other characters. This last seems to explain the various rates of evolution within a given taxanamic group and we can observe it by the fossil remnants of various ages. If large series of fossil Lepidtoptera would become available, there can be no doubt that this question, important to both stratigrapher and evolutionist, would probably be answered as follows:

Organisms of little variability in time will manifest little variability in space, and vice versa.

With an organism in the sense of F. E. Zeuner (1943), we will assume a fast transition from the "phylogenetic stage" X to Y and a minor variation in the process of formation of the recent form Z. In this way, the given form after a period of major differentiations, gives no changes in the future, or at least changes so small that they do not affect the taxonomic position of this form. Such forms have been called *phylogenetic relics* by B. B. Rohdendorf (1959). It is possible that recent butterflies of the genus *Pyrameis* are, thanks to their wide adaptive range, such phylogenetic relics that have colonized nearly the entire world.

It is also possible that study of variation in recent forms at various taxonomic levels will give insight into their formation and age. Such a study should be carried out based on complete and deep examination of recent material. And butterflies, in my opinion, are a most suitable subject for such a study.

The next question that may arise when fossil material is under consideration is the question of tempo in evolution of various organs and systems on the wing, as an anatomical unit. Study of our material suggests that time changes in the wing pattern occur more quickly than changes in venation. This, perhaps, may be explained by the fact that pattern in insects is a "younger" structure in comparison with venation. In this case we deal with phenomena much like those described by A. N. Severtzov (1936). This also relates to the previous thought expressed above, on the dependence between age and variability, but at the level of organs.

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REFERENCES

JACHONTOV, A. A. 1935. Our butterflies. Moscow. (In Russian).

EFREMOV, I. A. 1950. Taphonomy and geological record. Trudy *Paleont. Inst., 24.* (In Russian).

KASPIEV, B.F. 1939. Outcrops of teritiary insect-containing layers in the vicinity of Voroshilovsk Caucazsky. *Priroda,* 8: 75. (In Russian).

KOZHANTCHIKOV, I. V. 1957. A new representative of the family Cossidae from the Miocene deposits of Caucasus (Lepidoptera, Insecta). *Doklady Acad. Sci. U.S.S.R.,* 113(3): 675-677 (In Russian).

ROHDENDORF, B. B. 1939. On the Miocene insect fauna of the vicinity of Voroshilovsk. Priroda, 12: 85-88. (In Russian).

———— 1959. Phyogenetic relics. *Trudy Inst. Morph. Zhivotnykh Acad. Sci. U.S.S.R.,* 27: 41-51 (In Russian).

SEVERTZOV, A. N. 1936. Principal directions of the evolutionary process. Moscow. (In Russian).

STICHEL, H. 1909. 7. Gattung: *Pyrameis* Hbn. in: A. *Seitz, Grossschmetterlinge der Erde, I. Abt., 1.Bd.* (*Text*): 198-200.

SCHWANWITSCH, B. N. 1949. A course of general entomology. Moscow-Leningrad. (In Russian).

ZEUNER, F. E. 1943. Studies in the systematics of *Troides* Huebn. (Lepideptera, Papilionidae) and its allies; distribution and phylogeny in relation to the geological history of the Australian archipelago. *Trans. Zool. Soc. London,* 25(3): 107-187.